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Effects of Soils on the Holocene History of Forest Communities, Cape Cod, Massachusetts, U.S.A.

L'influence des sols sur l'évolution des communautés forestières à l'Holocène, au Cape Cod (Massachusetts, É.-U.)

Der Einfluß der Böden auf die Geschichte der Waldeinheiten im Holozän, Cape Cod, Massachusetts, U.S.A.

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Résumé de l'article

Les données palynoiogiques tirées d'une séquence sédimentaire dans le OwI Pond, à Cape Cod, atteste de la persistance d'une zone de végétation dominée par le pin blanc et le chêne pendant la plus grande partie de l'Holocène. Les petites superficies de la cuvette (1,6 ha) et de son bassin versant indique que la plus grande partie du pollen qui s'y dépose provient de la végétation des alentours; conséquemment, l'inventaire palynologique peut servir à étudier l'évolution des forêts environnantes. L'inventaire palynologique de 10 500 ans montre trois phases principales de stabilité relative de la végétation. La phase tardiglaciaire de forêts d'épinettes et de pins gris a été suivie, au début de l'Holocène, par une phase durant laquelle le pin blanc dominait le paysage et le chêne blanc et le pin rigide prenaient de plus en plus d'importance. Après 9000 ans BP, la forêt dominée par le chêne régnait, mais le pin blanc continuait à être un élément important. Ce patron ressemble aux changements de végétation survenus ailleurs dans le sud de la Nouvelle-Angleterre, sauf en ce qui a trait aux valeurs relativement élevées de pollen du pin qui reflète l'influence des sols glaciaires sablonneux du Cape Cod. On compare les données palynoiogiques du OwI Pond avec ceux du Duck Pond, également du Cape Cod. Les valeurs polliniques du chêne sont plus élevées au OwI Pond, mais les valeurs polliniques du pin rigide sont plus élevées au Duck Pond depuis 8000 ans. On considère que le type de sol (composition, texture) est le facteur le plus important dans les différences observées dans les deux sites. Les résultats tirés du site du Old Pond semblent indiquer que l'influence locale du substrat a permis, pendant l'Holocène, l'établissement de parcelles de végétation dominées par le chêne réparties ça et là au Cape Cod dans un paysage lui-même dominé par le pin rigide.

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EFFECTS OF SOILS ON THE HOLOCENE HISTORY OF FOREST COMMUNITIES, CAPE COD MASSACHUSETTS, U.S.A.

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ABSTRACT Palynological evidence from a sediment sequence in Owl Pond, Cape Cod, Massachusetts, documents the persistence of an area of oak-white pine dominated vegetation through most of the Holocene. The small size of the basin (1.6 ha) and its small catchment area suggest that it receives most pollen from nearby vegetation and consequently its pollen record can be used to study the history of the surrounding forests. The 10,500-year pollen record showed three main phases of relative vegetational stability. A late-glacial spruce-jack pine forest phase, followed by an early Holocene phase when white pine dominated the landscape while oak and pitch pine became increasingly important. After 9000 yr BP, an oak-dominated forest was established. White pine continued to be an important component of the forest. This pattern is similar to vegetational changes elsewhere in southern New England, except for the relatively high values of pine pollen, which reflect the influence of the sandy glacial soils on Cape Cod. The pollen record from Owl Pond is compared with that from another site on Cape Cod, Duck Pond. Oak pollen values are higher at Owl Pond, but values of pitch pine pollen are higher at Duck Pond for the past 8000 years. Soil type (composition, texture) is judged to be the most important factor in maintaining the differences between the two sites. The results from Owl Pond suggest that mainly through the local control of the substrate, a mosaic of oak-dominated patches of vegetation existed at places on Cape Cod during the Holocene, interspersed within a pitch pine-dominated landscape.

RÉSUMÉ *L'influence des sols sur l'évolution des communautés forestières à l'Holocène, au Cape Cod (Massachusetts, É.-U.).* Les données palynologiques tirées d'une séquence sédimentaire dans le Owl Pond, à Cape Cod, atteste de la persistance d'une zone de végétation dominée par le pin blanc et le chêne pendant la plus grande partie de l'Holocène. Les petites superficies de la cuvette (1,6 ha) et de son bassin versant indique que la plus grande partie du pollen qui s'y dépose provient de la végétation des alentours; conséquemment, l'inventaire palynologique peut servir à étudier l'évolution des forêts environnantes. L'inventaire palynologique de 10 500 ans montre trois phases principales de stabilité relative de la végétation. La phase tardiglaciaire de forêts d'épinettes et de pins gris a été suivie, au début de l'Holocène, par une phase durant laquelle le pin blanc dominait le paysage et le chêne blanc et le pin rigide prenaient de plus en plus d'importance. Après 9000 ans BP, la forêt dominée par le chêne régnait, mais le pin blanc continuait à être un élément important. Ce patron ressemble aux changements de végétation survenus ailleurs dans le sud de la Nouvelle-Angleterre, sauf en ce qui a trait aux valeurs relativement élevées de pollen du pin qui reflète l'influence des sols glaciaires sablonneux du Cape Cod. On compare les données palynologiques du Owl Pond avec ceux du Duck Pond, également du Cape Cod. Les valeurs polliniques du chêne sont plus élevées au Owl Pond, mais les valeurs polliniques du pin rigide sont plus élevées au Duck Pond depuis 8000 ans. On considère que le type de sol (composition, texture) est le facteur le plus important dans les différences observées dans les deux sites. Les résultats tirés du site du Old Pond semblent indiquer que l'influence locale du substrat a permis, pendant l'Holocène, l'établissement de parcelles de végétation dominées par le chêne réparties ça et là au Cape Cod dans un paysage lui-même dominé par le pin rigide.

ZUSAMMENFASSUNG *Der Einfluß der Böden auf die Geschichte der Waldeinheiten im Holozän, Cape Cod, Massachusetts, U.S.A.* Pollen- und Fossilbelege einer Ablagerungssequenz in Owl Pond, Cape Cod, Massuchsetts, dokumentieren das Fortbestehen eines von Eiche und Weißkiefer dominierten Vegetationsgebietes während des größten Teils des Holozäns. Die geringe Größe des Beckens (1.6 ha) und sein kleines Einzugsgebiet legen nahe, daß es den meisten Pollen von der umliegenden Vegetation erhält, und so kann sein Polleninventar für das Studium der Geschichte der umliegenden Wälder genutzt werden. Das Pollen-Inventar von 10 500 Jahren zeigte drei Hauptphasen relativer Vegetationsstabilität. Eine spätglaziale Rottanne- und Graukiefer-Waldphase, gefolgt von einer Frühholozänphase, in der Weißkiefer die Landschaft beherrschte, während Eiche und Pechkiefer zunehmend wichtig wurden. Nach 9000 Jahren v.u.Z. hatte sich ein von Eiche beherrschter Wald angesiedelt. Die Weißkiefer blieb ein wichtiger Bestandteil des Waldes. Dieses Muster ähnelt den Vegetationswechseln anderswo in Neuengland, mit Ausnahme der relativ kohen Kiefernpollenwerte, welche den Einfluß der sandigen glazialen Böden auf Cape Cod spiegeln. Der Pollenbeleg von Owl Pond wird mit dem eines anderen Platzes auf Cape Cod, Duck Pond, verglichen. Die Eichenpollenwerte sind bei Owl Pond höher, aber die Pechkieferpollenwerte sind für die letzten 8000 Jahre am Duck Pond höher. Man hält den Boden-Typus (Zusammensetzung, Textur) für den wichtigsten Faktor für die Aufrechterhaltung der Unterschiede zwischen den zwei Plätzen. Die Ergebnisse von Owl Pond legen nahe, daß hauptsächlich durch die örtliche Kontrolle des Substrats auf Cape Cod ein von Eiche beherrschtes Mosaik von Vegetationsflecken hier und da im Holozän existierte, welches in eine von Pechkiefer beherrschte Landschaft fein verteilt war.

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INTRODUCTION

In southern New England, Deevey (1939, 1943) first described postglacial vegetational change in terms of a 'classic' set of pollen zones (T, A, B, C), which record a sequence from tundra to spruce woodland, pine forest, and oak forest. With its distinct geologic character and its oceanic climate, Cape Cod has supported vegetation different from that to the west. Several investigators (Deevey, 1948; Belling; 1977; OKeefe and Patterson, 1980) have studied the pollen in peat deposits from the Cape. Winkler's (1982, 1985) pollen diagram from Duck Pond in South Wellfleet provides the longest regional record of vegetational change from Cape Cod. Her record extended back to 12,000 yr BP and showed a history of vegetation from boreal forest to northern conifer forest to a more mixed forest in which pitch pine and oak trees dominated the landscape. The sequence of vegetation changes is similar to the one documented on the mainland except for the persistently high values of pine pollen at Duck Pond throughout the Holocene.

This study presents the pollen and sediment record of the past 10,500 years, from Owl Pond, a kettle lake in Brewster, Cape Cod. Owl Pond is a small basin and consequently, receives most pollen from nearby vegetation. The history of small forested areas is better represented in the pollen records of such small basins (less than 5 ha) (Jacobson and Bradshaw, 1981; Bradshaw and Webb, 1985). The pollen record from Owl pond can thus be used to add detail to the vegetational history of the Cape.

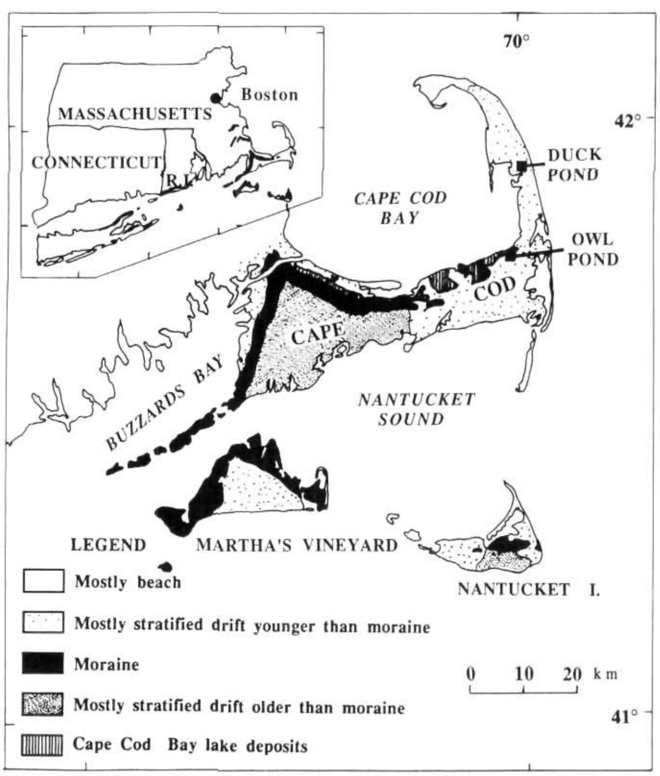


FIGURE 1. Generalized geologic map of Cape Cod and the islands (from Oldale and O'Hara, 1984). Inset map shows location of major end moraines in southern New England and Long Island.

Carte géologique généralisée du Cape Cod et des îles environnantes (de Oldale et O'Hara, 1984). Le carton donne la localisation des principales moraines frontales du sud de la Nouvelle-Angleterre et de Long Island.

Winkler (1982, p. 3) states that "Although a pond the size of Duck Pond (5 ha) does not receive appreciable pollen from areas outside a 10 km radius, ...pollen records at Duck Pond could be representative of those in a broader area because the topographic diversity and the edaphic characteristics of the pitted outwash plain around Duck Pond are similar to other outwash plains throughout the Cape."

According to Winkler (1982), pitch pine reforestation and present land-use practices have concealed any potential variation of vegetation composition that would be expected from local effects of the substrate. Was pitch pine forest as dominant and extensive during the entire Holocene as it is today? Alternatively, did any variability in physical factors lead to a mosaic of vegetation on the landscape, with areas of less xeric forest communities interspersed within a pitch pine-dominated forest? An attempt was made to address these questions by comparing pollen data from Owl Pond and Duck Pond. Local differences between the two profiles are highlighted by means of a difference diagram, a technique developed by Jacobson (1979) for comparing pollen sequences from sites in contrasting settings. Differences primarily in the relative abundances of oak and pine pollen between Owl Pond and Duck Pond are discussed in light of the edaphic characteristics around each lake. The effects of fire and pollen source area are also considered.

Vascular plant nomenclature follows Gleason and Cronquist (1963). All ages are in uncorrected radiocarbon years BP.

GEOLOGY, VEGETATION, AND SITE DESCRIPTION

Cape Cod is a peninsula composed of gravel, sand, and clay, that extends from southeastern Massachusetts into the Gulf of Maine (Fig. 1). The present form of Cape Cod is essentially a product of the Late Wisconsin Glaciation and the subsequent influence of marine processes. The drift on Cape Cod is part of the complex of end moraines and outwash plains that were deposited by the Wisconsinan ice in coastal areas of New York, Rhode Island and Massachusetts (Fig. 1, inset) (Oldale, 1982). The Late Wisconsinan ice front in southeastern New England was characteristically lobate. Differential retreat of ice lobes caused the development of a proglacial lake, which at its maximum extent occupied most of Cape Cod Bay. Inner Cape Cod, Nantucket, and Martha's Vineyard consist mostly of southward sloping outwash plains bordered on the north by ice-contact slopes or end moraines (Oldale, 1982). Lake deposits consisting of clay, silt, and fine to very fine sand are found north of the moraine and outwash plains (Oldale *et al.*, 1971). Outer Cape Cod consists of outwash plains that slope gently westward towards Cape Cod Bay (Fig. 1).

The time of deglaciation of Cape Cod has been a point of debate. Radiocarbon dates on basal organic material from kettle lakes and peat bogs range from 15,000 to 12,000 yr BP. These dates, even if they represent the actual radiocarbon age of the sample, should be treated only as minimum estimates. The degree to which a date indicates local deglaciation depends on the sedimentary regime in the basin following retreat of the ice and the relative stratigraphic position of the dated sample (King, 1985). For example, lakes that show evidence of stagnant ice blocks surviving buried under the drift should not be used in the reconstruction of ice recession, since the ice may have persisted for several hundreds or thousands of years before organic sedimentation could begin (Florin and Wright, 1969). Radiocarbon dates of about 14,000 yr BP from the late glacial marine clay near Boston (Kaye and Barghoorn, 1964) imply that the ice had already retreated from Cape Cod by that time. Stone and Borns (1986) correlate the Sandwich Moraine on Cape Cod with moraines in Connecticut and other recessional deposits in New Jersey that are younger than 18,570 yr BP. Retreat of the ice seems to have actually started in western Long Island before 18,000 yr BP, and morphostratigraphic relationships suggest that deglaciation began in the west and progressed eastward (Oldale, 1986). The implication is that the ice may have retreated from Cape Cod earlier than the radiocarbon dates indicate, possibly even by 16,000 yr BP.

The outwash plains on the Cape are 'pitted' with numerous deep hollows formed when buried blocks of stagnant ice melted beneath a cover of outwash sediment. Owl Pond near Brewster, Massachusetts (41°45'24"N, 70°15'30"W) is one of the many kettle lakes of the Inner Cape (Fig. 1). It is located in the Harwich outwash plain near the border with the lake deposits associated with the proglacial lake that occupied Cape Cod Bay. Owl Pond is a 1.6 ha lake lying 7.3 m above sea level, with a maximum depth of 9.1 m and no inflowing or outflowing streams.

The present vegetation of Cape Cod is mainly pitch pine (*Pinus rigida*) and oaks (scrub, *Quercus ilicifolia*; white, *Q. alba*; black, *Q. velutina*). Pitch pine, scrub oak, and also myricaceous and ericaceous shrubs are abundant on the predominantly sandy glacial substrate. Interspersed on the landscape, however, are patches of more mesophytic vegetation associated with moist hollows where the effects of salt spray and strong winds are less, and where fire frequency is reduced (Winkler, 1982, 1985).

The slopes surrounding Owl Pond support mainly pitch pine and, to a lesser extent, oak. One Atlantic white cedar (*Chamaecyparis thyoides*) grows on the northern side of the pond and so do a few scattered birch trees. Members of the heath (Ericaceae) and holly (Aquifoliaceae) families grow on the shores of the lake along with sweet gale (*Myrica gale*).

METHODS

FIELD AND LABORATORY METHODS

A square-rod Livingstone piston corer (Wright, 1967) was used to retrieve a 10 m sediment core from the centre of Owl Pond in 9 m water depth. For the uppermost 1 m, a polycarbonate core barrel was used to ensure accurate sampling of the sediment/water interface. The rest of the core was taken in one meter segments, which were extruded in the field, wrapped in plastic film, aluminium foil, and stored in a freezer.

Percent organic content of the sediment was determined gravimetrically by heating samples to 105°C and 550°C (Dean, 1974) (Fig. 3).

Standard treatments (Faegri and Iversen, 1975; Birks and Birks, 1980) were used to process 1 cm^3 samples for pollen analysis. A known quantity of *Lycopodium* spores was added as spike (Stockmarr, 1971). Samples were boiled in 10% KOH to remove soluble humic acids and to break down the sediment. Screening removed coarse debris. Samples were treated with 10% Hcl to remove carbonates and then boiled in hot HF for 30 minutes to remove silicates. Finally, samples were acetolysed (9 parts acetic anhydride: 1 part concentrated sulphuric acid) for 4.5 minutes to remove hydrolyse cellulose. The residue was mounted in silicon oil. On average, 400 grains were counted per slide. Pollen grain identifications were made using keys of McAndrews *et al.* (1973), and Richard (1970), and modern pollen reference slides.

Pine pollen grains were identified in two steps. First they were separated into subgenera, haploxylon and diploxylon pine types, based on the presence/absence of verrucate markings on the tenuitas (Ueno, 1958). Diploxylon pine grains were further separated by measuring the horizontal axis of the body plus the bladders. Following the procedure of Winkler (1982, 1985), grains smaller than 60 μm were tallied as jack pine (*Pinus banksiana*), and those larger than 75 μm as pitch pine (*Pinus rigida*). Grains of red pine (*Pinus resinosa*), with an average size of 63 μm, ranging from 53 to 73 μm (Bassett *et al.*, 1978), did not seem to be present. All pine separations were made on whole, reasonably well preserved grains; those that were broken, degraded, corroded, or whose tenuitas were ruptured, concealed by bladders, or obscured by debris, were not considered. The procedure described above was followed to ensure that the results (Fig. 4) were compatible with those from Duck Pond (Winkler, 1982, 1985).

NUMERICAL METHODS

Radiocarbon chronology. — Four samples were submitted for radiocarbon dating, their positions determined partly by the pollen stratigraphy and partly by the requirement for a set of evenly spaced dates to provide chronostratigraphic control (Table I; Steventon and Kutzbach, 1987). A date of 330±50 yr BP was asssigned to the 31 cm depth of the core, where percentages of ragweed (*Ambrosia*) pollen increased, indicating European settlement (Winkler, 1982).

Dates were assigned to the core by linear interpolation between ^{14}C dates (Fig. 2). A date of 10,430 yr BP was assigned by extrapolation to the base of the core at 912.2 cm. A second age model was developed to take into account the

TABLE I

Radiocarbon dates from Owl Pond (Steventon and Kutzbach, 1987).

Depth (cm)	Material	Radiocarbon age (yr BP)	Laboratory reference no.
195.0-204.0	gyttja	1180 ± 70	WIS-1868
393.7-401.7	gyttja	3190 ± 80	WIS-1867
589.5-597.5	gyttja	6819 ± 80	WIS-1866
892.1-903.9	gyttja	10,270 ± 140	WIS-1865

Radiocarbon ages have been calculated using the Libby half-life of 5568 for ^{14}C.

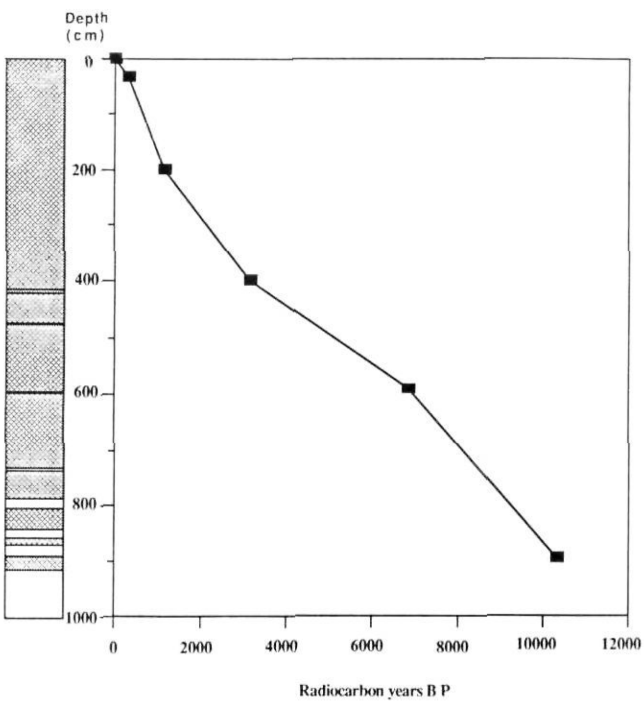


FIGURE 2. Core depths plotted versus radiocarbon age for the core. A date of 330 yr BP was assigned to the rise of ragweed pollen percentages near the top of the core, and a date of 0 yr BP was assigned to the top of the core. Lithology of the core included: stippled pattern indicates sand bodies; cross-hatched pattern indicates organic-rich sediments (gyttja).

Diagramme profondeur/âge. On attribue un âge de 330 BP à l'augmentation du pourcentage du pollen de l'ambroisie près du sommet de la carotte et un âge de 0 BP au sommet. Les trames donnent la lithologie: le pointillé identifie les sables et le quadrillé montrent les sédiments riches en matière organique (gyttja).

presence of sand lenses near the base of the core. These sand lenses, their thickness totalling 45.8 cm, were assumed to have been deposited instantaneously. Ages were interpolated along the organic mud layers, disregarding the sand lenses. The two control points for the interpolation were the same as in the first age model, *i.e.* the lowest two radiocarbon dates at 593.5 cm and 898 cm. In essence, a new slower sediment accumulation rate (0.0748 cm yr^{-1} versus the original 0.0881 cm yr^{-1}) was calculated for the organic-rich layers near the base of the core. This model provided slightly older dates below 593.5 cm, the amount of correction controlled by the position of the sand bodies. Ages mentioned in text are based on the second model.

Finally, for the pollen influx values, a cubic spline function was used which produced smoothed sediment accumulation rates. This was done in order to avoid sharp peaks in the curves which can lead to artificial changes in the sedimentation rates at the depths of the dates.

Pollen diagrams. — The pollen sum included pollen of terrestrial vascular plants. Unknown and indeterminable pollen and spores, and the pollen and spores of aquatic vascular plants were excluded. Pollen percentages and pollen accumulation rates appear in Figures 3 and 5, respectively.

Difference diagrams were prepared in order to compare the data from Owl and Duck Ponds (Fig. 6). This was done by linearly interpolating pollen percentages at specified dates (in this case at 500 year intervals) from the two chronologically closest pollen spectra that would bracket a designated date. Twenty two such interpolated spectra were generated. Following Bradshaw (1978) the measure of difference

$$\Delta p_{ik} = p_{1ik} - p_{2ik}$$

was used, where p_{ik} is the proportion of taxon k at the sampling position corresponding to time i at sites 1 (Owl Pond) and 2 (Duck Pond), respectively. This method "...requires a reliable and independent time control, so that similar periods of time are being compared" (Birks and Gordon, 1985, p. 137).

RESULTS AND DISCUSSION

SEDIMENT STRATIGRAPHY

The sediments are of two types: glacial sands and organic muds. The base of the core is characterized by interbedded organic and sand lenses (Fig. 3). The basal organic lens contains fibrous plant fragments but no formal identification of macrofossils has been made. The sands overlying the basal organic layer may have been deposited as ground surfaces collapsed due to differential melting of a stagnant ice block buried under outwash. Alternatively, the interbedding of sands and organic sediments may imply periodic inwash of mineral material into the basin perhaps as a result of frost action, solifluction and/or aeolian activity; this may have happened when continuous vegetation cover was not yet established and slopes around the lake were steep and unstable. A sample from the basal organic lens was dated at 10,270±140 yr BP. In comparison, the lowermost date from the Duck Pond sediments was 11,710±120 yr BP; a 'litter' layer containing aquatic mosses, aquatic plants and planktonic diatoms was reported from the basal sediments and was used as evidence of a stagnant ice origin of the lake (Winkler, 1982, 1985). If the date of *ca.* 16,000 yr BP for the deglaciation of Cape Cod is accepted, then the inferred buried ice block at Owl Pond persisted for approximately 5500 years, which seems to be an excessively long interval given the relatively small size of the lake. Florin and Wright (1969) have argued, however, for the persistence of buried dead ice for several thousand years at a site in Minnesota. In addition, Oldale and O'Hara (1984) and Oldale (1986) have inferred the role of permafrost in the formation of the thrust moraines on the Cape. They noted, however, that in the absence of any direct indicators (*i.e.* relict ice wedge features), the case for permafrost remains to be proved. According to Florin and Wright (1969), buried glacial ice can be considered thermally equivalent to permafrost in terms of the low temperatures needed to maintain it. It may then be possible to consider the persistence of small buried ice blocks for several thousand years similar to that at Owl Pond as indirect evidence for permafrost in Cape Cod, at least for part of the Late Glacial. The picture that emerges from the Cape during the Late Glacial is that of an unstable landscape with lakes forming at different times as ice blocks melted and the drift mantle along with any supraglacial vegetation collapsed; the situation may have been similar to that observed at present in the moraines of the Klutlan Glacier, Yukon Territory, Canada (*e.g.* Wright, 1980; Birks, 1980; Whiteside *et al.*, 1980). A different interpretation for the

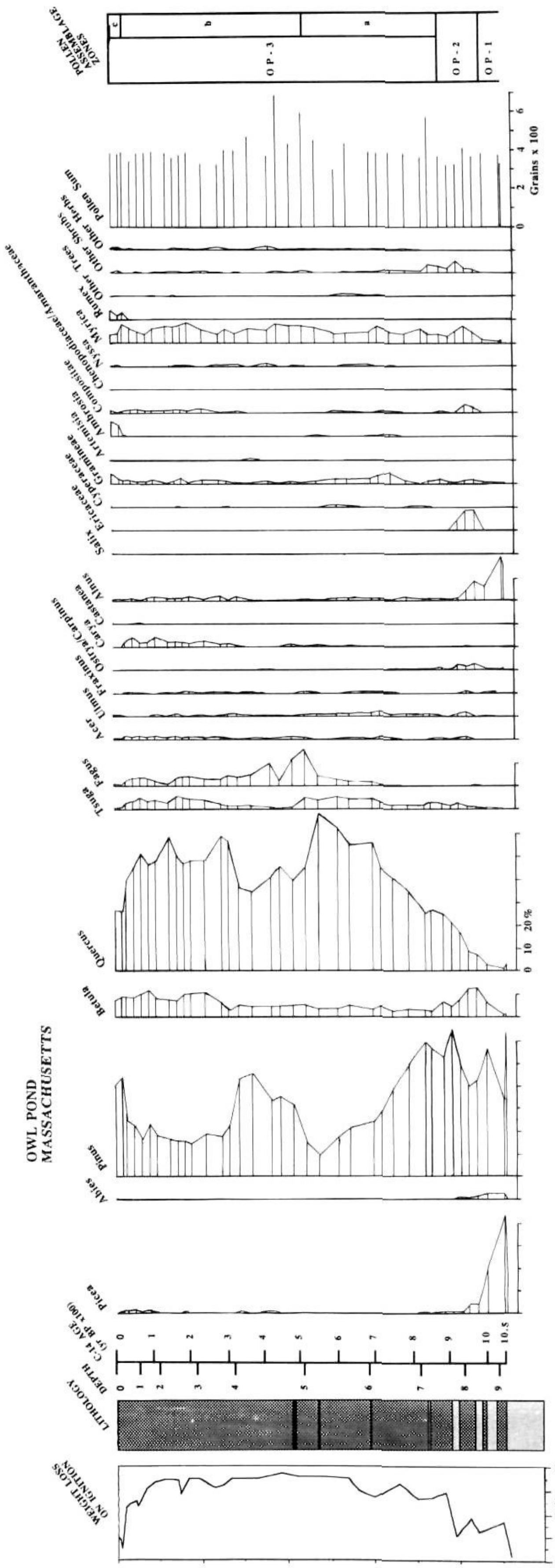


FIGURE 3. Percent organic content, lithology and selected pollen percentages for Owl Pond.

Teneur en matière organique (en %), lithologie et quelques pourcentages polliniques, à Owl Pond.

delay in the onset of organic sedimentation at Owl Pond may be possible, if the presence of sand lenses is taken to reflect past lake-level fluctuations. However, sediment stratigraphical examination and micro/macrofossil analysis on a spatial array of cores would be required for any reliable reconstruction (*e.g.* Digerfeldt, 1986). Given the position of the core at the centre of the basin, a lowered lake level scenario implies that the basin was dry, or nearly so, for a long period of time following deglaciation. Local palaeohydrological setting (*e.g.* water table level, relation of fresh to salt ground water, substrate) rather than regional conditions, must have been the controlling factor, in view of the approximately 1500-year difference in initiation of organic sedimentation between Duck and Owl Ponds.

Weight loss-on-ignition percentages (Fig. 3) indicate that the organic content of the sediment increases to over 50% above 770 cm (approximately 9100 yr BP). The percent fraction of the organic material remained high from 9000 yr BP onwards, until it decreased to low values above 20 cm. The high ash weight percentages (over 80%) encountered above 20 cm (*i.e.* over the past 200 years) reflect a marked increase in inorganic input to the lake associated with land-clearance practices (Davis, 1976). The increase in ash percentages associated with increases in minerogenic matter occurs at other levels in the core from Owl Pond. These increases could be associated with a forest fire and subsequent erosion, but detailed charcoal measurements must be made before any such conclusions can be drawn.

POLLEN STRATIGRAPHY

Following Cushing (1967), local pollen assemblage zones unique to Owl Pond were designated. The construction and definition of pollen zones should be viewed as a convenient way of displaying pollen analytical results and of facilitating comparison and correlation with other regional pollen sequences.

The results of numerical zonation (Tzedakis, 1987) agreed with the zonation derived by visual inspection of the pollen percentage diagram (Fig. 3). The diagram was divided into three pollen assemblage zones: (1) a spruce/pine/alder (*Picea/Pinus/Alnus*) zone (OP-1) from 10,480 to 10,100 yr BP (912 cm to 865 cm), (2) a (white) pine/birch (*Pinus (strobus)/Betula*) zone (OP-2) from 10,100 to 9000 yr BP (865 cm to 762 cm), and (3) an oak/pine (*Quercus/Pinus*) zone (OP-3) from 9000 yr BP to present (762 cm to 0 cm). Zone OP-3 was further divided into three subzones: OP-3a from 9000 to 5150 yr BP (762 cm to 504 cm), OP-3b from 5150 to 330 yr BP (504 cm to 30 cm), and OP-3c from 330 yr BP to present (30 cm to 0 cm).

Zone OP-1. — Spruce pollen percentages were at a maximum (43%), while pine pollen values were between 35 and 65%. Total pollen accumulation rates were between 40,000 to 60,000 grains cm^{-2} yr^{-1} and both spruce and pine had values of over 20,000 grains cm^{-2} yr^{-1}. Spruce pollen accumulation rates increased from 5000 to 21,000 grains cm^{-2} yr^{-1}, indicating the

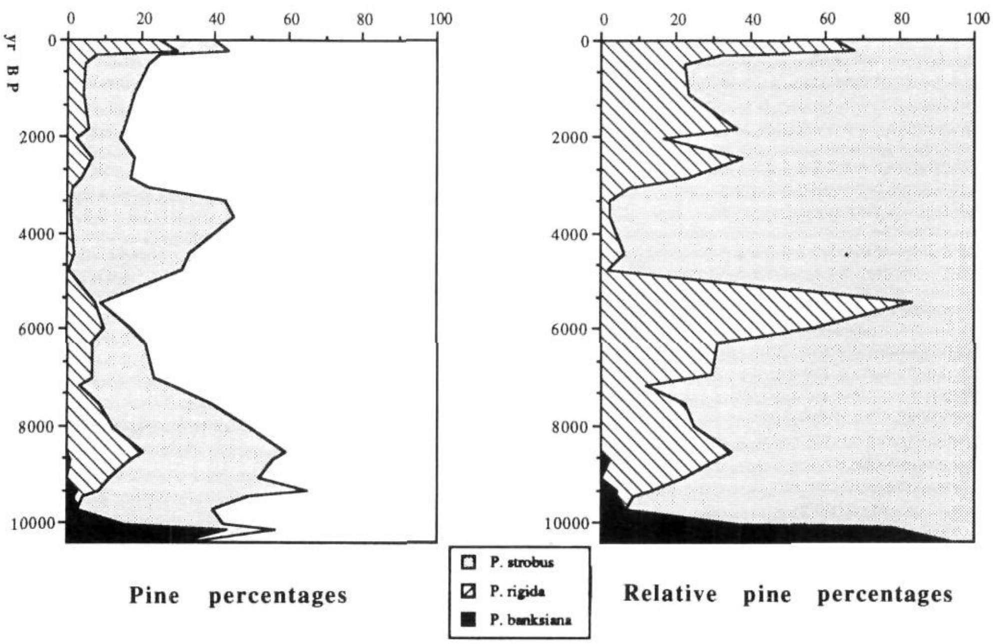


FIGURE 4. Pine species as percentages of the pollen sum and as relative pine percentages.

Les espèces de pin en pourcentages de la somme pollinique et en pourcentages relatifs.

establishment of spruce trees in the landscape. Spruce pollen percentages declined at the end of the zone while pine values increased. Most of the pine grains (approximately 85%) were identified as jack pine, while the rest were white pine (Fig. 4). The typical peaks in percentages of first alder (*A. crispa*) pollen at *ca.* 10,400 yr BP and then birch pollen (Gaudreau and Webb, 1985) occur in and just above this zone. The pollen evidence suggests a boreal forest environment. The results of an analogue search (Tzedakis, 1987), using the method of Overpeck *et al.* (1985), for comparing fossil samples with modern samples from 1850 sites in eastern North America, showed that the most similar samples of modern pollen were from sites north of 48°N, in the boreal forest of Ontario and Québec.

Zone OP-2. — This zone is characterized by high values of pine pollen (40-65%) and a peak in birch pollen. Jack pine values decreased dramatically after 10,000 yr BP (Fig. 4), while white pine became the most important pine (over 90% of all pine grains counted). Pitch pine pollen appeared for the first time about 9500 yr BP and gradually increased in importance (Fig. 4). High birch pollen abundances, probably representing white birch (*B. papyrifera*) populations (Gaudreau and Webb, 1985), occur in this zone, with maximum pollen percentage and influx values (12% and 8600 grains cm^{-2} yr^{-1}, respectively) recorded around 9650 yr BP. Oak pollen percentages gradually increased to 25% by the end of this zone. Total pollen accumulation rates ranged between 44,000 and 92,000 grains cm^{-2} yr^{-1}. Myricaceae pollen percentages increased to 5-7% and remained approximately stable through the rest of the sequence. Values of Ericaceae pollen peaked at 9% and 6000 grains cm^{-2} yr^{-1}.

The pollen data suggest that in this zone white pines dominated the forests with birch trees being also important. Oak trees became increasingly important after 9500 yr BP. The appearance of pitch pine pollen indicates that the density of pitch pines around Owl Pond had by that time reached a level detectable by pollen analysis. The first indications of pitch pine pollen at Duck Pond were also at about 9500 yr BP (Winkler, 1985). The high values of Myricaceae pollen indicate the beginning of continuous growth of these shrubs near the pond. The unusually high values of Ericaceae pollen suggest that wetlands may have surrounded the ponds or that ericaceous shrubs grew in the pine forests. A similar peak in Ericaceae pollen values is recorded at Duck Pond at the time (Winkler, 1982, 1985).

Zone OP-3. — This zone is generally characterized by high values of oak pollen. At the onset of subzone OP-3a the highest total pollen accumulation rates (96,000 grains cm^{-2} yr^{-1}) are recorded, a time of high abundances of pine and oak, both taxa being prolific pollen producers (Bradshaw and Webb, 1985). By 8500 yr BP jack pine disappeared completely, while pitch pine percentages peaked accounting for 20% of the total pollen sum (Fig. 4). Oak pollen percentages gradually increased to reach high values of over 60% towards the end of the subzone. This increase indicates the progressive competitive replacement of pines by oak trees in the landscape. Pine percentages decreased to low values (9%) after 6000 yr BP Accumulation rates for pine pollen were as low as 1400 grains cm^{-2} yr^{-1}. Most of the pine grains deposited at that time were of the pitch pine type (Fig. 4). Hemlock (*Tsuga*) pollen percentages steadily increased to reach values of 5% by 6000 yr BP. Beech (*Fagus*) pollen percentages increased by the end of subzone 3a.

The beginning of subzone OP-3b is marked by an abrupt decline in hemlock values to less than 1%. This "hemlock decline" is generally found to be a synchronous pollen stratigraphic event in eastern North America, and Davis (1981) attributed it to a forest pathogen. Webb (1982) showed that the dates for this event are normally distributed with a mean of 4650 yr BP and a standard deviation of 300 years. The dates he used were interpolated from the "mid-point between the two adjacent samples between which the percentages of *Tsuga* pollen decreased the most" (Webb, 1982, p. 569). The comparable hemlock decline at Owl Pond occurred around

4950 yr BP and falls within the uncertainty of the dating of this event. The low abundances of hemlock persisted for almost two thousand years. Beech percentages increased to 16% at the beginning of the subzone, about 5100 yr BP, a time of maximum beech pollen frequencies in New England (Bennett, 1985). Oak values decreased somewhat and then increased again, but in general stayed over 40%. Pine pollen percentages began increasing at the onset of this subzone and reached a high of 45% about 3600 yr BP. White pine was again important on the landscape and its pollen accounted for over 90% of all pine (Fig. 4). An abrupt decrease in total pine pollen values from 40% to 20% occurred after 3300 yr BP, while oak pollen percentages increased to 56%. During the rest of the subzone, total pine pollen values stayed below or near the 20% level with pitch pine increasing slightly (Fig. 4), while oak pollen values remained high, fluctuating about 50%, but decreasing towards the end of the period. Hickory (*Carya*) pollen frequencies increased during this period for the first time to levels of 2.5%. Hemlock percentages increased steadily after 3000 yr BP and reached pre-decline values after 2400 yr BP.

The pollen assemblages of the above two subzones reflect the increasing importance of deciduous forest trees around Owl Pond. This pattern is similar with vegetational changes occurring in southern New England (Gaudreau and Webb, 1985). Persistently high values of pine pollen, however, are not generally encountered ouside the Cape and reflect the influence of the sandy glacial soils on the Cape.

In subzone OP-3c, herbaceous pollen increased markedly to 10%, while oak percentages decreased. Pine values increased during the last 200 years, with the ratio of pitch pine pollen to white pollen pine becoming approximately 2:1. This probably reflects the reforestation of the Cape in the early 1800's, after the early period of rapid forest clearance: pitch pine was planted and grass was used to stabilize the forest dunes (Thoreau, 1849/1985; Winkler, 1982). Pre-1800's farming practices led to the depletion of the organic humus of soils. Pitch pine was favoured over white pine during reforestation because of its competitive ability to survive on the less fertile soils following farm abandonment. Organic content of the sediment decreased to less than 20% percent in the upper 10 cm of the core (Fig. 3). In general, the pollen changes and the increase in inorganic input in this subzone reflect the effect of human disturbance on the landscape after European settlement in the 17th century.

COMPARISON OF OWL POND AND DUCK POND

The pollen sequences from the Owl and Duck Ponds are compared by means of a difference diagram (Fig. 6). The method removes the common regional signal and emphasizes differences at a finer scale of vegetation. Given the small size of the basins and their respective catchment areas, the results of this comparison should reflect differences in local and extra-local (*sensu* Jacobson and Bradshaw, 1981) vegetation.

Spruce pollen percentages were higher at Owl Pond between 10,500 and 10,000 yr BP (Fig. 6). This could be interpreted as indicating that the spruce period ended later at Owl Pond than at Duck Pond. The geographic proximity (20 km) of the two sites, however, suggests that this lag probably arises from imperfections in the age model. The initial age model showed a 650 year time difference for the end of the spruce period at the two sites. The second age model, which took into account the presence of sand lenses, reduced this difference for the same event to 250 years, which is within the standard error associated with the dates. In addition, the lowermost radiocarbon sample at Owl Pond (Table I) was taken from the organic lens that contained the 'litter' layer, where bank collapse and sediment slumping may ultimately be responsible for the dating inconsistencies. Other biostratigraphic events, however, such as the end of the pine pollen assemblage zone, or the appearance of pitch pine pollen, appear to occur more or less synchronously at the two sites.

The most striking feature of the difference diagram is the persistently higher values of oak pollen for the past 8000 years (with difference values up to 35%) at Owl Pond, and the higher values of pine pollen at Duck Pond. Difference values for total pine pollen are higher at Duck Pond, reaching a maximum of 33%. This difference mainly reflects the overall importance of pitch pine as the dominant tree around Duck Pond throughout the Holocene. White pine never attained dominant status during the Holocene at Duck Pond. In contrast, at Owl Pond white pine was the most important conifer during the Holocene. White pine abundances in the landscape fluctuated, decreasing after the pine period (OP-2: 10,100 to 9000 yr BP), then increasing again between 5000 and 3000 yr BP when it became the forest dominant, and decreased after that. Differences in other taxa are an order of magnitude smaller, with no particular trends apparent for any one taxon at any of the sites. Hemlock values tend to be somewhat higher at Owl Pond (0.5 to 3%).

Distinct substrate types are known to support distinct vegetation. According to Buckman and Brady (1969) the texture of soil material is the most important factor determining water and nutrient properties. These properties, in turn, influence competitive balances among plant species. The soil surrounding Duck Pond were classified as Carver sands by the U.S. Department of Agriculture Soil Conservation Service (1987). These are excessively drained soils that form in deep deposits of coarse and very coarse crystalline sand. In contrast, the soils surrounding Owl Pond have been classified as Plymouth-Barnstable Complex (PxB) (USDA Soil Conservation Service, 1987). PxB is defined as a complex of a variety of soils which are extremely bouldery and having silt and clay in the upper surface; also described as loamy sand containing a mixture of sand, silt, and clay particles, it has finer texture than Carver sands. The implication is that as the fineness of the texture increases, moisture and nutrient levels also increase. In contrast, Carver sands are prone to leaching which removes the organic humus from the surface (Strahler, 1966). The capacity of humus to hold water and nutrients is great and thus small amounts of humus augment greatly the capacity of soils to support plant growth (Buckman and Brady, 1969).

The soils surrounding Duck Pond are not fertile and only few species can survive. According to Fowells (1965, p. 405) "pitch pine is usually restricted to the less fertile, those of shallow depth or of sandy texture". Since it can withstand a range of moisture values and can grow on excessively drained sands, its high values around Duck Pond during most of the Holocene

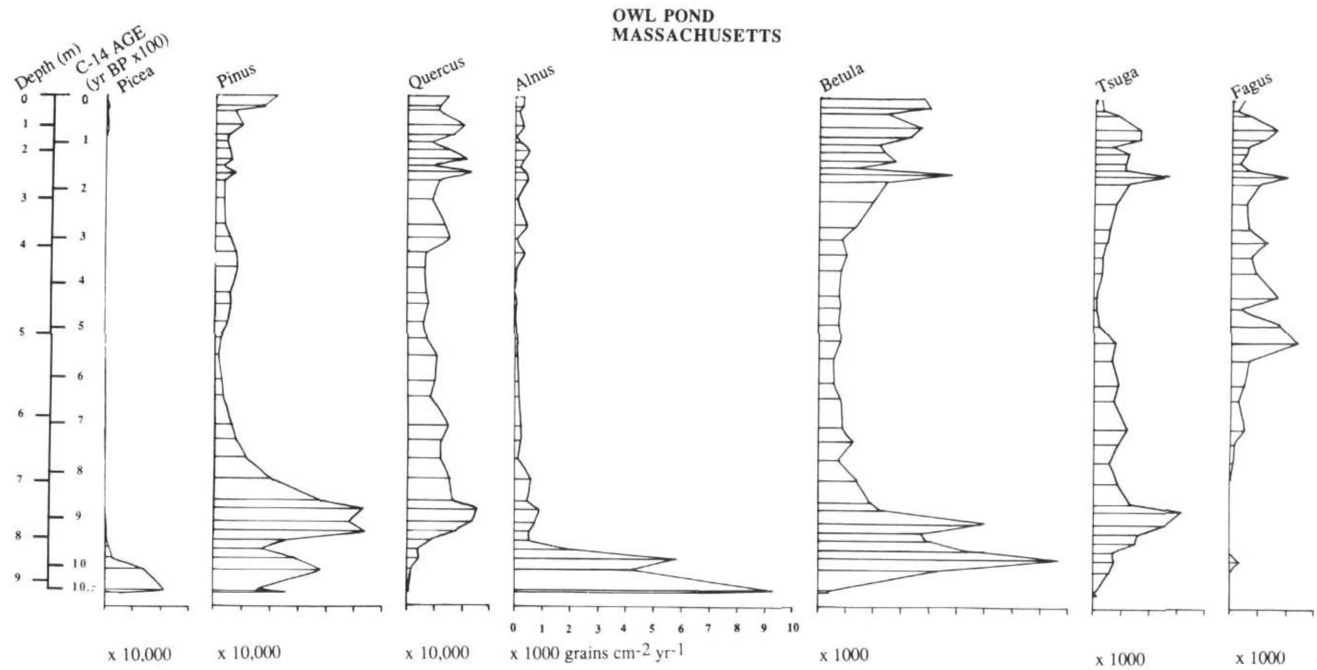


FIGURE 5. Pollen accumulation rates for selected taxa, total pollen concentration, and total pollen accumulation rates.

Les taux d'accumulation pollinique pour quelques taxons choisis, la concentration pollinique totale et les taux d'accumulation pollinique totale.

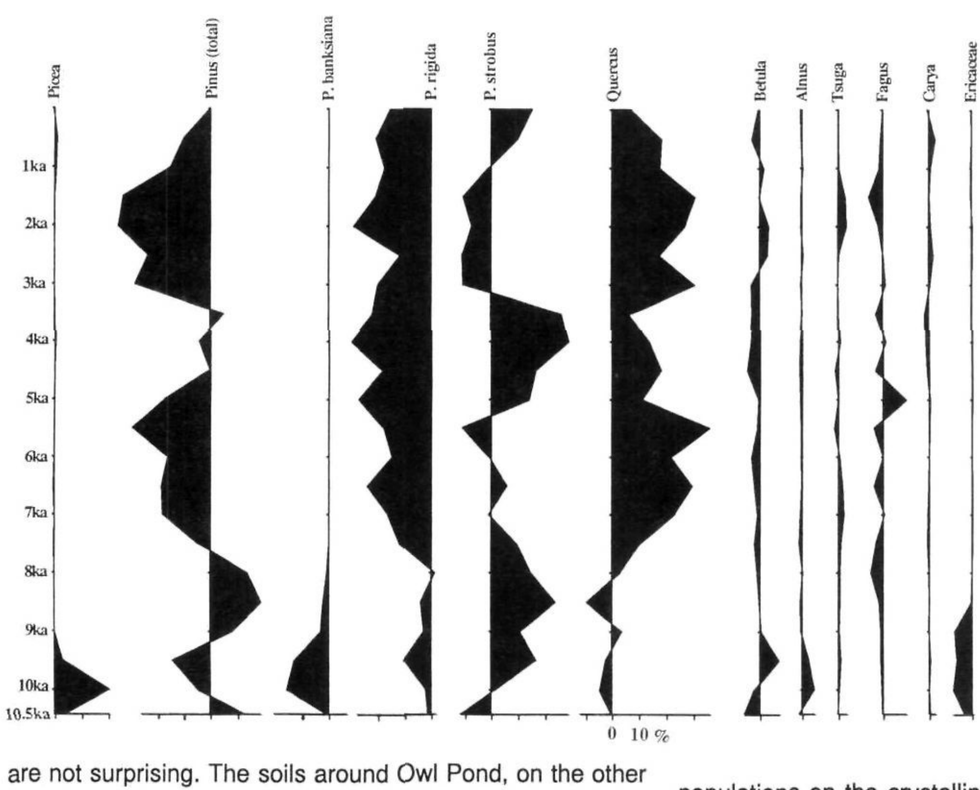
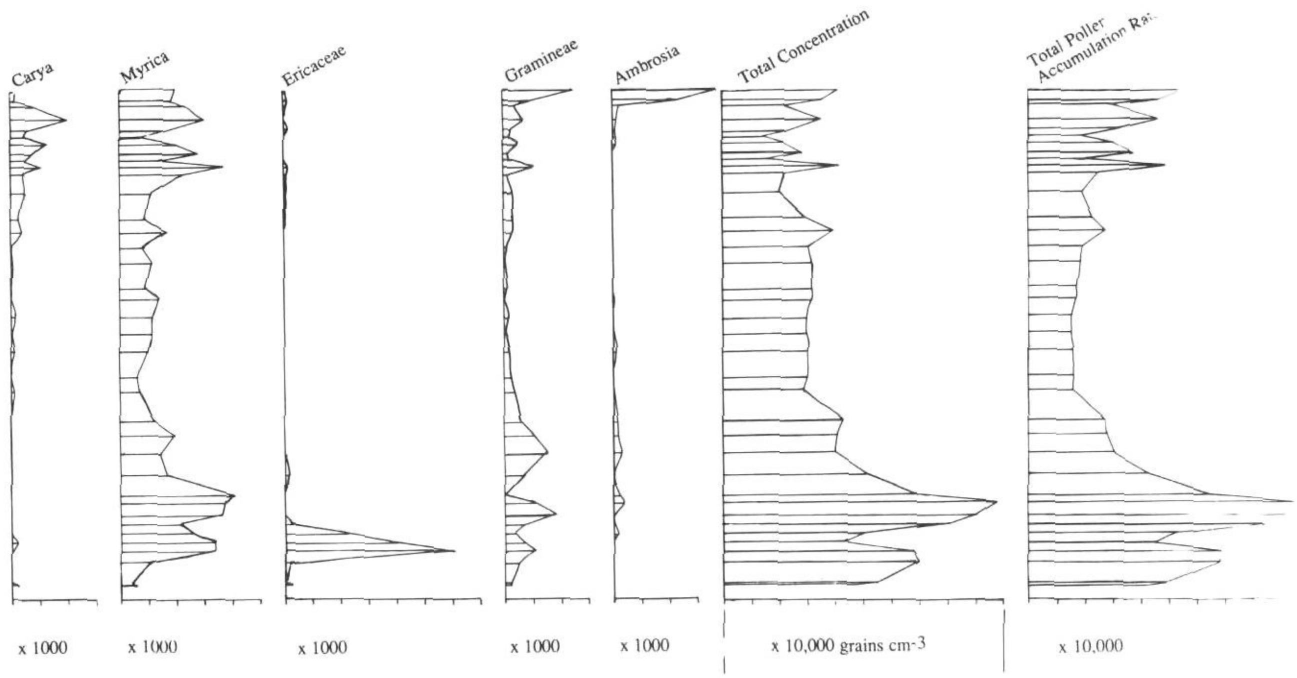


FIGURE 6. Difference diagram for selected taxa (Owl Pond minus Duck Pond pollen percentages). Positive values for a pollen type indicate percentage greater at Owl Pond. Negative values indicate percentage greater at Duck Pond.

Diagramme des différences pour quelques taxons choisis (pourcentages polliniques du Owl Pond moins ceux du Duck Pond). Les valeurs positives pour un type pollinique donné indique un pourcentage plus élevé à Owl Pond; les valeurs négatives indiquent un pourcentage plus élevé au Duck Pond.

are not surprising. The soils around Owl Pond, on the other hand, are more fertile and can support a more diverse vegetation. The identification of pine pollen to species level has shown that white pine was dominant around Owl Pond. Pitch pine pollen values were important (in relation to other pine species) around Owl Pond, when percentages of total pine pollen were low. These pitch pine pollen values may actually represent long distance transport from well-established pitch pine populations on the crystalline outwash plains. Alternatively, they may reflect a few trees in the immediate catchment.

Similar substrate control on the composition of Holocene plant communities has been extensively documented in the palaeoecological literature. For example, Brubaker (1975) found in northern Michigan that diploxylon type pines (jack pines) occupied the well-drained sandy soils of the Yellow Dog



outwash plain, whereas white pine was predominantly found in the deciduous-coniferous woods on the moister soils of the Michigamme outwash and on the Michigamme till. Jacobson (1979) used difference diagrams to compare paired sites located on contrasting soil types in Minnesota. Sites located on sandy outwash displayed high values of diploxylon (red/jack) pine, while sites located on tills showed that white pine was an important component within a generally more mesic forest. Table II summarizes the influence of soils on the vegetation as demonstrated in the two papers mentioned above, and shows how their results compare with the findings of the present study.

Fires have an important influence on forest communities by opening land for invading species and by maintaining stands of fire-resistant species. Fire disturbance might have provided openings for white pine and hardwoods to invade and become established. According to Green (1981, 1987) hardwoods, which have a lower flammability, tend to reduce fire frequency and intensity, thus further allowing fire-sensitive species to spread. Grimm (1984) discussed fire probability in terms of a number of abiotic and biotic factors. Of these factors, macroclimate, topography, and size of physiographic unit are the same or similar for Owl and Duck Ponds. Soil texture differences can be important: coarse-textured soils, which retain little moisture, have a greater rate of biomass drying and, consequently, a higher fire probability. Another factor that can lead to potential differences between the two sites is the composition of vegetation and its flammability. As mentioned earlier, hardwoods are less flammable than conifers. The Holocene forest around Duck Pond was dominated by pitch pines. According to Fowells (1965, p. 406) pitch pine "is outstanding... in its ability to survive [fire] injury". It is associated with sites where fires are too frequent for other species to attain dominance. Wright and Bailey (1982) note that in the absence of fire white pine, oak, and hemlock may supplant pitch pine. The frequency of fire occurrence may, therefore, account at least in part for the differences between the two sites. The establishment of pitch pine around Duck Pond can be thought of as setting a positive feedback mechanism: the pitch pine forest has a higher propensity to fire outbreaks; this drives out fire-sensitive species, thereby leading to purer stands of pitch pine which favour even more frequent fires. The reverse situation may have occurred in the case of Owl Pond, where the fine-textured soils led to a moister site with a lower fire incidence, in turn, leading to the establishment of mixed white pine-hardwoods stands with lower fire resistance. Unfortunately, detailed measurements of charcoal concentrations from Owl Pond are not available, and the effect of fires on the forests around the two ponds cannot be assessed. Bearing in mind that the proposition of higher fire frequency around Duck Pond has to await confirmation, the extent to which fires influenced the composition of Holocene vegetation can still be considered. Although fire occurrence must have influenced the vegetation, it is difficult to envisage fire alone as an agent capable of continuously maintaining vegetational differences between the two sites for approximately 8000 years, given general changes in Holocene macroclimate.

Finally, the influence of the size of the pollen catchment areas may be examined. Jacobson and Bradshaw (1981) have summarized theories and evidence for the relationship between pollen source area and basin size. It is generally accepted that there is a positive relationship between lake surface area and size of the pollen source area. The areas of Owl Pond and Duck Pond are 1.6 and 5 hectares respectively. Accordingly, Owl Pond may be receiving a large part of its pollen from trees growing on the compositionally diverse and generally finer soils near the pond. These soils make up approximately 64% of the area within a 1 km radius around Owl Pond. They seem capable of having supported a more mesic forest throughout the Holocene. Duck Pond, on the other hand, may receive a greater amount of far-travelled pollen. Pine pollen makes up a considerable portion of this regional pollen because of (a) its excellent dispersal properties, which allow it to travel often

TABLE II

Sites on contrasting soils and dominant Holocene tree taxa

Site	Reference	Long. (degrees, minutes)	Lat. (degrees, minutes)	Basin size (ha)	Distance between sites (km)	Soil type/landforms	Dominant Holocene tree taxa
Yellow Dog	Brubaker (1975)	46 45 N	87 57 W	1.50		well sorted medium sands/ Yellow Dog outwash	jack pine
					5		
Lost Lake	Brubaker (1975)	46 43 N	87 58 W	1.00		silt + clay, sands-moist soils/ Michigamme outwash	white pine
					7		
Camp II Lake	Brubaker (1975)	46 40 N	88 01 W	1.50		silt + clay, sand, gravel-heavy soils/ Michigamme till	deciduous-coniferous
Willow River Pond	Jacobson (1979)	46 20 N	92 47 W	0.65		fine red sand/Willow River outwash	jack pine
					12		
Nelson Pond	Jacobson (1979)	46 24 N	92 41 W	1.78		red clay till/Nickerson moraine	white pine, hardwoods
Duck Pond	Winkler (1985)	41 56 N	70 00 W	5.10		coarse crystalline sands/ Wellfleet outwash plain	pitch pine
					20		
Owl Pond	Tzedakis (this paper)	41 45 N	70 15 W	1.60		loamy sands, finer texture/ Harwich outwash plain	oak, white pine

much further than 1 km, and (b) the fact that the greater area surrounding Duck Pond is characterized by coarse-crystalline sands that can support pitch pine-dominated forests. Theoretical considerations by Prentice (1988) on the effect of basin size on pollen source area, however, suggest that the difference in size between Owl Pond and Duck Pond is too small to have any real effect on the pollen catchment area. Work by Jackson (1990) on pollen source area and representation in very small lakes (<0.5 ha) in southern New England and northern New York, has shown that the local and extralocal component of the pollen rain they received was much less than that predicted by the Jacobson-Bradshaw (1981) model. Significant amounts of oak and pine pollen originated from distances greater than 500 m from the lake shores. It appears, therefore, that Owl and Duck ponds sample approximately similar size areas of vegetation and that differences in basin size do not have a serious effect on differences between the two pollen profiles.

CONCLUSIONS

1) The sediment sequence at Owl Pond contains a record that extends back to 10,500 yr BP. The pollen record reveals three distinct phases in the vegetation history around Owl Pond: a spruce-jack pine dominated forest from 10,500 to 10,000 yr BP; this was replaced by a white pine forest in which oak and pitch pine gradually became important. After 9000 yr BP an oak forest with increasing abundances of more mesic taxa (hemlock, beech, maple, ash, hickory) was established, while white pine continued to be important in the landscape. At the end of the third period, European disturbance and replanting led to a marked increase of herbs and pitch pines.

2) The results from Owl Pond were compared with those from Duck Pond, also on Cape Cod. The comparison revealed consistent differences between the two sites throughout the Holocene. The record from Duck Pond reflected a pitch pine-dominated forest, while the record from Owl Pond suggested that a more mesic oak-white pine forest was established in the area. Three physical factors that were different for the two sites were considered in order to explain the observed variation in vegetation: substrate, fire occurrence, and pollen catchment area. Differences in the size of the two basins are unlikely to have any appreciable effect on the pollen source areas, especially for pine and oak. Fire may have helped in perpetuating the pitch pine forest around Duck Pond. Of the three physical factors invoked to explain the vegetational differences between Owl Pond and Duck Pond, substrate is judged to have had the greatest influence. Even when the effects of pollen source area and fire frequency were considered, it was through the indirect influence of soils that these factors were important. At this spatial scale, where both sites share the same macroclimate and physiography, soil type (composition, texture) can control local vegetation patterns. Substrate is the sole factor which can have a substantial impact on vegetation and, moreover, whose influence could persist continuously and maintain the differences in forest composition between the two sites throughout the Holocene.

3) The pollen record from Duck Pond documents the existence of an extensive pitch pine-dominated forest on the sandy soils of the glacial outwash plains of Cape Cod during the greater part of the Holocene. The evidence from Owl Pond, however, shows that interspersed within the same region were areas that supported a more mesic vegetation. This mosaic of forest communities persisted mainly through local control of the substrate. Sites comparable in size to Owl Pond can sense the finer scale composition of vegetation and can be used to add detail to the history of forest communities on Cape Cod. Knowledge of the general vegetational history of a region can be based on sites selected for the extralocal and regional component of the pollen rain that they receive and/or for their edaphic and topographic characteristics which are representative of the region. At a finer scale, small lake basins located on diverse soils and topography can provide additional information on the extent of variability in vegetational patterns within the same region.

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